Impact of bark beetle outbreak on epigeic communities of Collembola (Insecta: Entognatha) in climax spruce forests in the Šumava National Park, Czech Republic

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Soil surface activity of epigeic communities of Collembola were studied in undamaged climax spruce forests, in dead spruce forests after bark beetle attack and in clearings in the Šumava National Park, South Bohemia, Czech Republic. Five pitfall traps were exposed at each of the nine study sites. They were exposed for 12 months during summer, fall and winter periods from 1999 to 2000. More than 149 000 specimens of Collembola belonging to 54 species were trapped, determined and evaluated. The highest epigeic activity of Collembola was in the summer period in the undamaged spruce forests (624.2 ind./trap/30 days), lower in the dead forests (604.1 ind./trap/30 days) and lowest in the clearings (549.8 ind./trap/30 days). The undamaged spruce forests had 19, whereas dead forests only 14 and clearings 17 characteristic species with constancy C > 49 %. *Allacma fusca, Dicyrtomina minuta, Sminthurinus aureus, Desoria neglecta, Desoria violacea* and *Xenylla maritima* reached their highest activity in undamaged forests. The best living conditions for *Tetracanthella stachi, Entomobrya nivalis, Tomocerus minutus, Parisotoma* cf. *agrelli, Ceratophysella denticulata, Pseudachorutes corticilola* and *Deutonura conjuncta* were in the dead forests. Highest epigeic activity in the clearings was exhibited by *Entomobrya lanuginosa, Lepidocyrtus cyaneus, Heterosminthurus bilineatus, Pseudisotoma sensibilis* and *Sminthurus nigromaculatus* belonging mostly to the atmobiotic life-form group characteristic of grasslands. The clearings had a drastic negative effect on the epigeic collembolan fauna found in the climax spruce forests whereas in the dead forests most of the epigeic species were positively influenced.

Keywords: Climax spruce forests, dead forests, clearings, epigeic Collembola, bark beetle outbreak.

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Introduction

Climax spruce forests are predominant in the Šumava National Park, South Bohemia, Czech Republic. In recent decades, these forests were attacked and heavily destroyed by bark beetles (mainly *Ips typographus* L.). As a result of the bark beetle calamity, there are large areas with dead trees. Two different management practices were applied on the damaged spruce forests. In highly protected Zone I of the National Park, the dead forests were left without felling. In the less protected Zone II, all dead trees were cut down and the logs removed. These clearings were planted to spruce, beech and rowan seedlings. A multi-disciplinary scientific project was developed and focused on the impact of both types of management practices, comparing the forests with standing dead trees, the clearings and the undamaged climax spruce forests. The soil zoological component of the project dealt with some groups of mesofauna (Collembola, Protura, Oribatida, Pauropoda), macrofauna (Oniscidea, Diplopoda, Chilopoda) and megafauna (Lumbricidae), and especially with epigeic representatives of these groups. The eight most dominant epigeic species of Collembola were handled in an earlier paper (Brůhová and Rusek, 2005). The present contribution is focused on the influence of the bark beetle outbreak and different forest management practices on the epigeic collembolan communities in these three habitats: climax spruce forests, dead forests, and clearings.

The main goals of our study were:

1. To study the activity of all epigeic species of Collembola in (a) undamaged climax forests (b) dead uncut spruce forests, and (c) clear cut spruce forests in the Šumava National Park;
2. To describe changes in epigeic activity in the studied species of Collembola;
3. To relate these changes in epigeic activity to spruce forest management after the bark beetle outbreaks.

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Material and methods

The investigations were carried out in the south-western part of the Czech Republic in the Šumava National Park, South Bohemia, in the area delimited by mounts Studená hora, Březník, Špičník and Blatný vrch. The whole Šumava (Bohemian Forest) mountain system together with adjacent parts in Bavaria and Austria forms one geomorphological unit consisting of crystalline shales, granites and syenitediorites. All experimental sites are located between 1180-1310 m a.s.l. Soils are represented by cambisolic podsols, and podsols predominate above 1250 m a.s.l. Many of the climax spruce forests have boggy organic soils dominated by *Sphagnum* moss. The climate is distinctly cool, the mean annual temperature above 1300 m a.s.l. is 3°C and the annual precipitation 1400 mm (Culek, 1996).

List of localities

Nine experimental plots were chosen with the following letter/number designation for each locality. These plots were about 50-200 m apart within an area 3 x 2.5 km.

Undamaged climax forests:

E0: SE slope, 1 km south of the Ptačí nádrž near Malá Mokrůvka, 1210-1220 m a.s.l., plant community *Calamagrostio villosae-Piceetum fagetosum*.

A0: S slope of Studená hora, 1255 m a.s.l., plant community *Calamagrostio villosae-Piceetum fagetosum*.

Dead forests:

EL1: SSW slope under the road Roklanská hájovna, 1240 m a.s.l., former plant community *Calamagrostio villosae-Piceetum fagetosum*.

EL2: SE slope of Pytlácký roh, 1260 m a.s.l. former plant community *Calamagrostio villosae-Piceetum fagetosum*.

AL1: W slope between Špičník and Březník, former plant community *Calamagrostio villosae-Piceetum fagetosum*.

AL2: SSE slope of Pytlácký roh, 1310 m a.s.l. former plant community *Calamagrostio villosae-Piceetum fagetosum*.

Clearings:

The former plant communities in the clearings were the same as in the undamaged climax spruce forests and they have changed after the clear cuts.

AP1: SSE slope of Studená hora, 1240 m a.s.l., plant community *Junco effusi-Calamagrostietum villosae*.

AP2: SW slope near Roklanská nádrž, 1185 m a.s.l., plant community *Junco effusi-Calamagrostietum villosae*.

EP2: S slope of Studená hora, 1240 m a.s.l., plant community *Junco effusi-Calamagrostietum villosae*.

Methods

Pitfall traps filled with formaldehyde were used for epigeic activity studies of soil fauna, including Collembola. The traps were constructed according to Absolon et.al. (1994) and modified by Tajovský (1996). Five traps were placed in the specified nine localities and exposed for 12 months during the summer (08. 06. 1999 – 12. 08. 1999), fall (12. 08. 1999 – 05. 10. 1999) and winter periods (05. 10. 1999 – 06 .06. 2000). The content of each pitfall trap was stored in 38% formaldehyde and, after sorting, Collembola were transferred into 96 % ethanol. Some species of Collembola with distinct colour patterns and clearly visible morphological characters were counted directly using a dissection microscope, other species required examination in microscopic slides using a phase contrast microscope with higher magnification. Microscopic slides were prepared according to Rusek (1975). Material of more than 149 000 specimen of Collembola belonging to 54 species was determined and evaluated.

Data analysis

The surface activity of the dominant collembolan species was statistically evaluated using the non-parametric Kruskal-Wallis test. A polythetic classification was produced by Two Way Indicator Species Analysis [TWINSPAN version 2.1 (Hill, 1979)] to classify the samples. Canonical Correspondence Analysis (CCA) was performed for log (n+1) transformed data using CANOCO version 4.5 (Ter Braak and Šmilauer, 1992). Parameters for constancy C, dominance D and activity A (Tischler, 1949) were calculated for each period: summer (Cs, Ds, As), autumn (Ca, Da, Aa) and winter (Cw, Dw, Aw). Epigeic activity of collembolan species was re-calculated for one trap and 30 days from each treatment.

Results

Forty-seven species of Collembola were collected in the pitfall traps from the undamaged live spruce forests (LF – in Figs. 1 and 2), but only 10 of them reached epigeic activity higher than 10 ind./trap/30 days [*Allacma fusca* (Linné, 1758), *Ceratophysella armata* (Nicolet, 1841), *Entomobrya* sp.juv., *Entomobrya nivalis* (Linné, 1758), *Hypogastrura socialis* (Uzel, 1891), *Lepidocyrtus lignorum* (Fabricius, 1781), *Pogonognathellus longicornis* (Müller, 1776), *Sminthurinus aureus* (Lubbock, 1862), *Vertagopus* spp. and *Xenylla maritima* Tullberg, 1869]. Fifty species of Collembola were trapped in the dead spruce forests (DF- Figs. 1 and 2), but only 11 of them reached epigeic activity higher than 10 ind./trap/30 days [*Ceratophysella armata*, *Entomobrya* sp. juv., *Entomobrya nivalis*, *Lepidocyrtus lignorum*, *Pogonognathellus longicornis*, *Protaphorura* spp., *Sminthurinus aureus*, *Sminthurinus niger* (Lubbock, 1868), *Tetracanthella stachi* Cassagnau, 1959, *Tomocerus minutus* (Tullberg, 1876) and *Sminthurinus niger*]. Forty-seven species of Collembola were collected in pitfall traps from the clearings (CL – Figs. 1

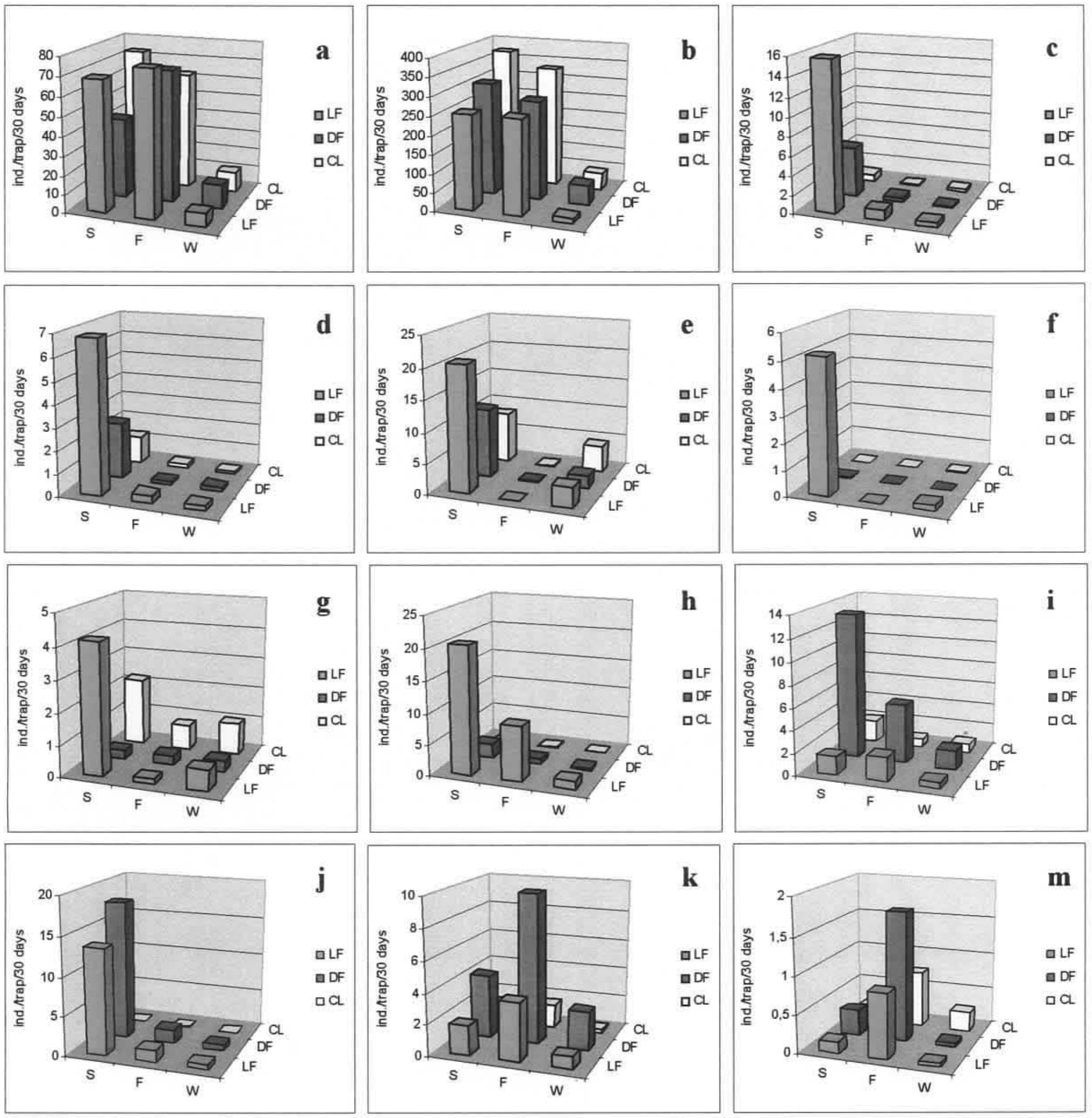

Fig. 1. Epigeic activities of individual collembolan species in undamaged climax spruce forests (LF), dead forests (DF) and clearings (CL) in summer (S), fallow (F) and winter (W) periods. a – *P. longicornis*, b – *L. lignorum*, c – *A. fusca*, d – *D. minuta*, e – *S. aureus*, f – *D. neglecta*, g – *D. violacea*, h – *X. maritima*, i – *T. stachi*, j – *E. nivalis*, k – *T. minutus*, m – *P.* cf. *agrelli*.

and 2), but only six of them reached epigeic activity higher than 10 ind./trap/30 days [*Entomobrya lanuginosa* (Nicolet, 1841), *Heterosminthurus bilineatus* (Bourlet, 1842), *Lepidocyrtus cyaneus* Tullberg, 1871, *Lepidocyrtus lignorum*, *Pogonognathellus longicornis*, and *Sminthurinus niger*].

Different epigeic activities of individual collembolan species show their habitat preference to undamaged climax spruce forests, dead forest or clearings, as well as to the seasons of the year (Figs. 1 and 2). *Pogonognathellus longicornis* (Fig. 1a) and *Lepidocyrtus lignorum* (Fig. 1b) exhibited high epigeic activity in both summer and fall seasons, nevertheless it was not significantly different among undamaged forests, dead forests and clearings. *Allacma fusca* (Fig. 1c), *Dicyrtomina minuta* (O. Fabricius, 1783) (Fig. 1d), *Sminthurinus aureus* (Fig. 1e), *Desoria neglecta* (Schäffer, 1900) (Fig. 1f), *Desoria violacea* (Tullberg, 1876) (Fig. 1g) and *Xenylla maritima* (Fig. 1h) reached their highest activity in undamaged forests. The best living conditions for *Tetracanthella stachi* (Fig. 1i), *Entomobrya nivalis* (Fig. 1j), *Tomocerus minutus* (Fig. 1k), *Parisotoma* cf. *agrelli* (Delamare Deboutteville, 1950) (Fig. 1m), *Ceratophysella denticulata* (Bagnall,

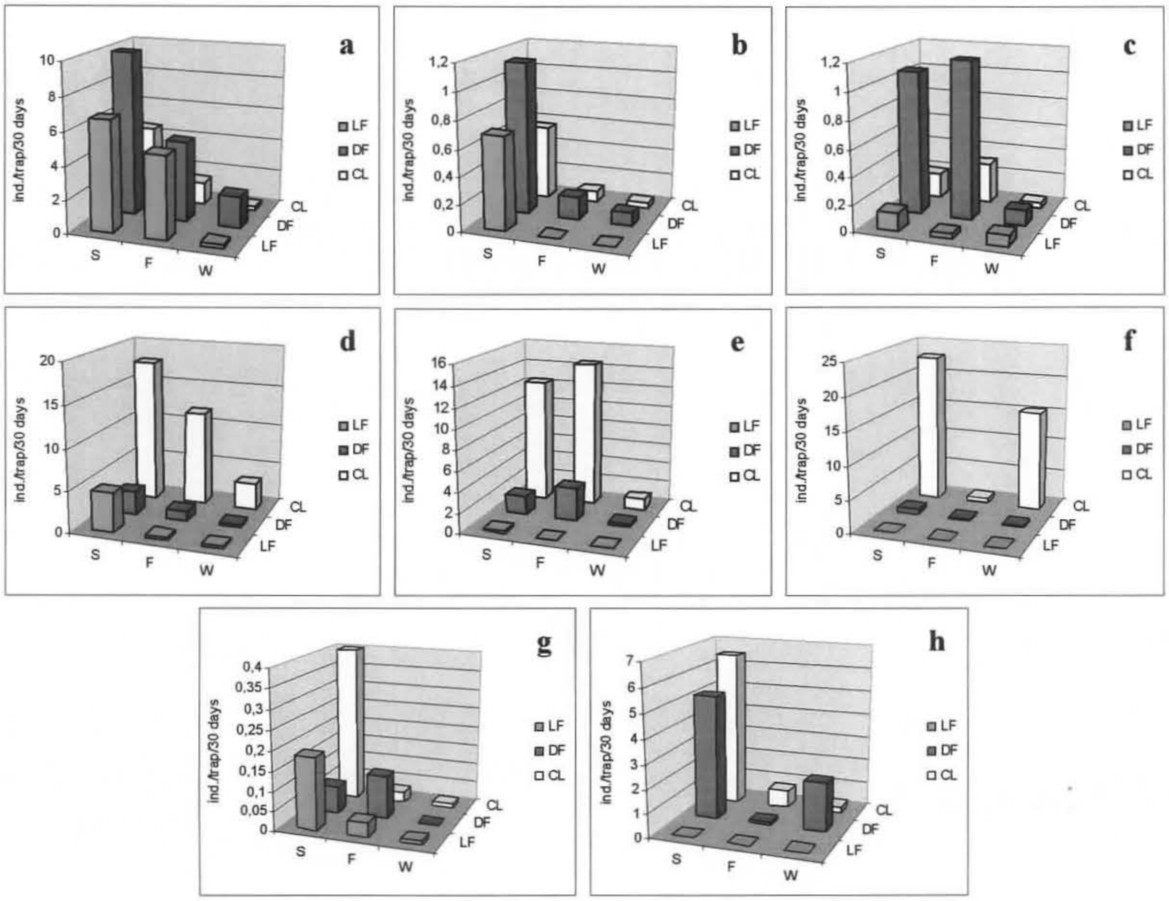

Fig. 2. Epigeic activities of individual collembolan species in undamaged climax spruce forests (LF), dead forests (DF) and clearings (CL) in summer (S), fallow (F) and winter (W) periods. a – *C. denticulata*, b – *P. corticifola*, c – *D. conjuncta*, d – *E. lanuginosa*, e – *L. cyaneus*, f – *H. bilineatus*, g – *P. sensibilis*, h – *S. nigromaculatus*.

1941) (Fig. 2a), *Pseudachorutes corticilola* (Schäffer, 1896) (Fig. 2b) and *Deutonura conjuncta* (Stach, 1926) (Fig. 2c) were seen in the dead forests where they exhibited the highest epigeic activity. Only a few species exhibited their highest activity in the clearings: *Entomobrya lanuginosa* (Fig. 2d), *Lepidocyrtus cyaneus* Tullberg, 1871 (Fig. 2e), *Heterosminthurus bilineatus* (Fig. 2f), *Pseudisotoma sensibilis* (Tullberg, 1876) (Fig. 2g) and *Sminthurus nigromaculatus* Tullberg, 1871 (Fig. 2h). These belong mostly to the atmobiotic life-form group and are characteristic of grasslands. Only a few epigeic species exhibited high epigeic activity in the winter season. TWINSPAN analysis of the summer series of collembolan epigeic activities showed *A. fusca,* already at the first level of division, as a characteristic species of undamaged forests (E0 and A0) and in one of the young dead forests (AL1). The absence of *L. cyaneus* in undamaged forests and of *E. nivalis* in the dead forests is related to epigeic activity, which is also seen in the summer series. The same was confirmed by the CCA for the summer epigeic activity series (Fig. 3).

The Collembola reaction to forest die-off depended on the species. Some forest species decreased their activity in dead forests (*A. fusca, D. minuta, S. aureus, D. violacea, D. neglecta, P. atra, C. armata, X. maritima, H. socialis* and *P. subcrassus*). Most of them decreased their activity, in some cases drastically, when the forests were cut down. Many species that became established in the clearings are common epigeic or atmobiotic grassland inhabitants and are typical of such ecosystems in the Šumava National Park, e.g. meadows, forest edges, and drier parts of peat bogs.

Discussion

Soil surface dwelling Collembola, as established in our study, could be arranged into 3-4 groups according to their reaction to changed environmental conditions such as dead spruce forests caused by bark beetle attack, and by huge clear cut areas of spruce forests and their further development in extreme microclimatic conditions. The first group includes species with the highest activity in the climax spruce forests, decreased

activity in dead forests and lowest activity (or absence) in clearings. *A. fusca* (Fig. 1c) and *D. minuta* (Fig. 1d) represent this category of forest species. Their highest epigeic activity was in the undamaged climax spruce forests (15.69 ind./trap/30 days for *A. fusca*, 6.83 ind./trap/30 days for *D. minuta*) and the lowest on the clearings (0.74 ind./trap/30 days for *A. fusca*, 1.26 ind./trap/30 days for *D. minuta*). Forest preference and the reason for high epigeic activity are known for *A. fusca*. The first larval stage is very susceptible to low air humidity (Betsch and Vannier, 1977) and apparently insufficient moisture levels in the clearings is a limiting factor for its larval development. Forest species with increasing epigeic activity in the dead forest belong to the second group. It is necessary to specify here, that the "dead forests" are not completely dead. Only bark-beetle attacked spruce trees died. This insect enemy did not attacked spruce seedlings, young spruce trees, as well as individual old spruce trees and rowan trees! Nevertheless, about 90 % of the spruce trees died off in the dead spruce forests and this added a 4-5 cm thick layer of spruce litter on the soil surface. The reduced tree transpiration led to an increased soil water content and to a rapid growth of understory plants (ferns, *Luzula sylvatica*, *Calamagrostis villosa*, etc.). During the first decade following the spruce forest die off, rotting dead trees begun to fall down to the soil surface. An environment suitable for many forest species of the above-mentioned second group was established in this way. To this group belong *Tetracanthella stachi* (Fig. 1i) (epigeic activity in spruce forests1.62 ind./trap/30 days, whereas 13.23 ind./trap/30 days in dead forests) *Entomobrya nivalis* (Fig. 1j) (epigeic activity in spruce forests13.52 ind./trap/30 days, whereas 17.91 ind./trap/30 days in dead forests), *Tomocerus minutus* (Fig. 1k) (epigeic activity in spruce forests 1.89 ind./trap/30 days, whereas 4.47 ind./trap/30 days in dead forests), *Ceratophysella denticulata* (Bagnall, 1941) (Fig. 2a) (epigeic activity in spruce forests 6.69 ind./trap/30 days, whereas 9.96 ind./trap/30 days in dead forests), *Pseudachorutes corticicola* (Schäffer, 1896) (Fig. 2b) (epigeic activity in spruce forests 0.69 ind./trap/30 days, whereas 1.15 ind./trap/30 days in dead forests) and *Deutonura conjuncta* (epigeic activity in spruce forests 0.14 ind./trap/30 days, whereas 1.11 ind./trap/30 days in dead forests). The following belong to the third group of species: *L. lignorum* (Fig. 1b) and *P. longicornis* (Fig. 1a) they were by far the most active species on all three habitats (not significantly different) showing a great ecological plasticity. The fourth group is typical for clearings: *Entomobrya lanuginosa* (Fig. 2d), *Lepidocyrtus cyaneus* Tullberg, 1871 (Fig. 2e), *Heterosminthurus bilineatus* (Fig. 2f), *Pseudisotoma sensibilis* (Tullberg, 1876) (Fig. 2g) and *Sminthurus nigromaculatus* Tullberg, 1871 (Fig. 2h). These species mostly represent the atmobiotic life-form group and are characteristic of grasslands.

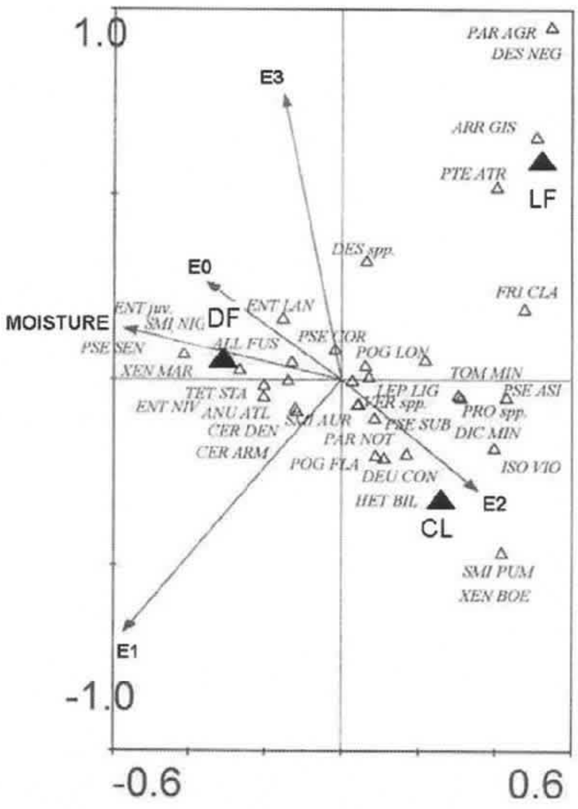

Fig. 3. CCA analysis for the summer epigeic activity series of the Collembola communities. Black triangles: LF – live, undamaged spruce forests, DF – dead forests, CL – clearings; E0 – E3 and MOISTURE: environmental variables; small white triangles: place of individual species of Collembola in the analysis quadrants. Species abbreviations: *ALL FUS – Allacma fusca, ANU ATL – Anurophorus atlanticus, ARR GIS – Arrhopalites gisini, CER ARM – Ceratophysella armata, CER DEN – Ceratophysella denticulata, DES NEG – Desoria neglecta, DES spp. – Desoria* spp., *DEU CON – Deutonura conjuncta, DIC MIN – Dicyrtomina minuta, ENT juv. – Entomobrya* juv., *ENT LAN – Entomobrya lanuginosa, ENT NIV – Entomobrya nivalis, FRI CLA – Friesea claviseta, HET BIL – Heterosminthurus bilineatus, ISO VIO – Desoria violacea, LEP LIG – Lepidocyrtus lignorum, PAR AGR – Parisotoma* cf. *agrelli, PAR NOT – Parisotoma notabilis, POG FLA – Pogonognathellus flavescens, POG LON – Pogonognathellus longicornis, PRO spp. – Protaphorura* spp., *PSE ASI – Pseudachorutella asigillata, PSE COR – Pseudachorutes corticicola, PSE SEN – Pseudisotoma sensibilis, PSE SUB – Pseudachorutes subcrassus, PTE ATR – Ptenothrix atra, SMI AUR – Sminthurinus aureus, SMI NIG – Sminthurinus niger, SMI PUM – Sphaeridia pumilis, TET STA – Tetracanthella stachi, TOM MIN – Tomocerus minutus, VER spp. – Vertagopus* spp., *XEN BOE – Xenylla boerneri, XEN MAR – Xenylla maritima.*

Some of the collembolan species with epigeic activity studied here are restricted to spruce forests or to clearings. Species living in climax spruce forests could be ecologically or eco-physiologically restricted to this habitat, whereas others could find more favourable conditions in the dead forests with higher soil humidity, less temperature and light fluctuations and surplus of food (decomposing needle litter).

Conversely, other factors (e.g., extreme microclimatic fluctuations, wind variation, soil-water changes, soil surface and plant cover exposed to sun radiation, etc.) enable only specialised atmobiotic and epigeic species to live in clearings. Clearings are the least favourable habitats for most forest species. Epigeic and atmobiotic species of Collembola have different colonization strategies for occupying new habitats and territories. Wind or water transportation is most efficient for the above-mentioned ecomorphic groups of Collembola. Forest species will be successful only in cases when they reach forest or dead forest habitats, but they will die off when they land in clearings. Only a few selected xerothermic epigeic species will be successful in colonizing new clearings. In the later stages of succession of clearings, the species spectrum will be extended for grassland atmobiotic and epigeic species. Most of the former hemiedaphic and especially euedaphic forest species will die off in the first few years after forest clear cutting, as was established during recent studies (Rusek, 2007).

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